UNIVERSITY OF CALIFORNIA
COLLEGE OF AGRICULTURE
AGRICULTURAL EXPERIMENT STATION
BERKELEY, CALIFORNIA

BREEDING FOR EGG PRODUCTION

LEWIS W. TAYLOR and I. MICHAEL LERNER

BULLETIN 626

October, 1938

UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA

CONTENTS

BREEDING FOR EGG PRODUCTION[1]

LEWIS W. TAYLOR[2] AND I. MICHAEL LERNER[3]

THE PURPOSE of this bulletin is twofold: (1) to review the present knowledge of the genetics of egg-production and egg-quality characters and (2) to demonstrate what may be accomplished by the application of the principles and methods discussed in the text in bringing about rapid improvement in egg production. For this purpose, data from the California Agricultural Experiment Station flock, as well as from literature on poultry breeding, are used.

In the limited space of a bulletin, only a small part of the published work on the subject can be reviewed. Only those papers which are directly drawn upon are cited. Similarly, the analysis of the Experiment Station data has necessarily been confined to the more important general considerations, with many details omitted. These data confirm in a striking manner the adequacy of the progeny-test method of breeding poultry, when this method is applied to the individual characters affecting production and viability. We believe that the application of similar principles should enable a poultry breeder to accomplish substantially the same type of flock improvement. The presentation of dogmatic methods of procedure for pedigree breeders has purposely been avoided because conditions vary widely from flock to flock. Emphasis is thus laid on broad principles which may be adapted to specific circumstances found in different flocks. However, a more definite breeding program for multipliers' flocks is advanced.

EXPLANATION OF TERMS USED IN BREEDING

Inheritance of characters is based on the transmission of genes from parent to offspring. *Genes* are defined as the determiners of hereditary characters. They occur in pairs (with a few exceptions), one member of each pair being derived from the sire, and its mate from the dam.

One member of the pair may be different from its mate, as in the case of a cross between two breeds. For example: A bird resulting from a cross between a purebred rose-combed and a single-combed bird will receive a gene for rose comb from one parent and for single comb from the other. The crossbred bird will exhibit a rose comb, since the rose-comb gene is

[1] Received for publication April 19, 1938.

[2] Associate Professor of Poultry Husbandry and Associate Poultry Husbandman in the Experiment Station.

[3] Instructor in Poultry Husbandry and Junior Poultry Husbandman in the Experiment Station.

dominant and prevents the expression of the single-comb gene, which is known as a *recessive.* If two such crossbred birds are mated together, in the next generation both rose- and single-combed individuals will appear in the ratio of three rose-combed birds to one single-combed bird. Of the rose-combed birds, one-third will be pure-breeding, and two-thirds will not breed true (possessing like their parents, one rose-comb gene and one single-comb gene). The birds which possess two like genes and breed true are *homozygous* for this gene. In the example given, the pure-breeding rose-combed and the single-combed birds are homozygous for comb-shape genes. Those rose-combed birds which possess two unlike genes will not breed true and are *heterozygous.*

Various genes are usually designated by arbitrary letters. Capital letters indicate the dominant condition, and small letters the recessive: the gene for rose comb, for example, is represented as *R* and that for single comb as *r*. The actual constitution of an individual with respect to these genes is known as the *genotype,* which is designated by the genes of which it is composed: the genotype of the single-combed bird, for example, is represented by *rr,* that of the pure-breeding rose-combed bird by *RR,* and that of the heterozygous rose-combed bird by *Rr.*

The appearance of the bird with respect to these characters is called the *phenotype.* In the example given, there are only two phenotypes—single-comb, to which the bird with the *rr* genotype belongs, and the rose-comb, to which the birds with both the *RR* and *Rr* genotypes belong. The two genotypes that show the rose-comb phenotype can be distinguished only by breeding tests. If a rose-combed bird, bred to a single-combed bird gives only rose-combed offspring, then it must belong to the *RR* genotype, but if it gives some single-combed offspring, then it must belong to the *Rr* genotype.

At times, when two unlike genes are present in the pair governing the expression of a character, neither gene completely suppresses the action of its mate. The case is then one of *incomplete dominance.* When this occurs, the mating of two such heterozygous individuals produces three phenotypes in the offspring, which correspond to the three genotypes present.

In cases where characters are produced by the action of a large number of genes, such are known as *multiple genes.*

Sex-linked inheritance can probably be best explained by an example. A simple sex-linked character in poultry is the barred plumage of the Barred Plymouth Rock. When a male of this variety is crossed with a black female, all the progeny is found to be barred. In a reciprocal cross, however, when a black male is mated to a barred female, in the first gen-

eration, the females are found to be black, while the males are barred. Sex-linked crosses for early sex identification are based on this principle.

The reason for the behavior of the sex-linked genes lies in the fact that the male possesses a paired complement, as in the case of all other genes, while the female has only one member of a sex-linked gene pair. Thus the male genotype in the case of the pure Barred Plymouth Rock is *BB,* while the female genotype is *B*–. In the case of the black birds, the male's constitution is *bb* and the female's *b*–. In the second cross as described above, $bb \times B-$ (black male × barred female), the male progeny will be heterozygous barred (*Bb*) and the females will be black (*b*–).

HISTORICAL DEVELOPMENT OF METHODS OF POULTRY BREEDING

The history of the development of egg-production characters in strains of chickens goes back centuries before there was any indication of a commercial poultry industry. The types of fowl developed in the countries bordering on the Mediterranean Sea were early recognized to have a greater inherent capacity for producing eggs than birds from the Orient. From these higher-producing fowl, the breeds of the Mediterranean class of chickens, which includes Leghorns, Minorcas, and Anconas, were developed. During an intensive period of breed creation in the nineteenth century, fowls of the Mediterranean class were extensively used to cross with Asiatic breeds or with mongrel stocks to produce new breeds and varieties, which are found in the American and English classes of chickens.

With the development of improved systems of transportation and marketing, accompanied by an increased demand for eggs for human consumption at seasons other than those of normal high egg production, an increasing importance was attached to the inherent ability of birds to lay. Under some conditions of poultry keeping, the value of a breed no longer rested entirely on its size and quality of meat, on its plumage color or pattern, or on its peculiar appearance as evidenced by structural differences in comb, feathers, or number of toes. Thus, by the middle of the nineteenth century, writers on poultry subjects began to emphasize the ability of certain breeds to lay a relatively large number of eggs. Before the end of that century, the idea of trapnesting birds in order to obtain exact records had been conceived and suitable devices to accomplish this work had been invented.

At the close of the nineteenth century, an experimental approach to the solution of problems involved in improving egg production was made by Gowell at the Maine Agricultural Experiment Station on a flock of

Barred Plymouth Rocks (Pearl and Surface, 1909).[4] His method of breeding involved the selection and mating of his better-producing females in one line and of the poorer in another. No means of evaluating the contributions of the breeding males was employed. After a period of years, the egg production in the two lines was approximately the same.

Pearl succeeded Gowell and was able to improve the production of the same flock by the use of different methods of selection. He noticed that there was a close correlation between the winter and the annual production of any bird. The more eggs produced in winter, the higher was the annual record. Using winter production as a criterion of selection for mating, and analyzing his results genetically, Pearl (1912) developed his theory of the inheritance of egg production, which proposed that two pairs of genes were primarily responsible for high egg production.

A few years after Pearl's work was published, Goodale (1918) introduced a new concept regarding the mode of inheritance of egg production obtained from studies on the Rhode Island Red flock of the Massachusetts Agricultural Experiment Station. Egg production was considered by him to be the final expression of the action and interaction of a number of diverse production characters. Of some ten characters first listed by Goodale, five are important in contributing to an individual's annual record. A sixth has been suggested recently. These characters may be divided into two general groups: those affecting the length of time the bird lays eggs, and rate or intensity of production when the bird is laying. The first group of characters include: the time when a pullet begins to lay eggs, known as *sexual maturity;* the time when a hen ceases to lay at the end of the pullet year of production, known as *persistency;* and the intervening nonlaying periods within the time limits of sexual maturity and persistency produced by *broodiness* and *winter pause. Spring* or *summer pause* may be considered as another character (Lerner and Taylor, 1936). These characters governing the length of time in production, combined with *rate of production,* determine the annual record of the hen.

After the development of the idea of breaking egg production down into a number of component parts, Goodale and later Hays carried on studies to determine the method of inheritance of these characters. As a result of these studies, Hays has advanced a series of hypotheses regarding the number and nature of the genes that control the characters determining egg production (see Jull, 1932, for a bibliography of papers on this subject). Hays and Sanborn (1934) also have published data on the improvement in the flock egg production and the various production

[4] See "Literature Cited" at the end of this paper for complete data on citations, which are referred to in the text by author and date of publication.

characters in the Massachusetts Station flock over a period of twenty years of breeding conducted by Goodale and Hays.

Several other investigators have published data on improvement in egg production. Dryden (1921), by breeding from hens with high egg records, was able to increase greatly the average production in the Barred Plymouth Rock, White Leghorn, and crossbred flocks at the Oregon Agricultural Experiment Station. He also commented that the use of the progeny test in selection might be expected to hasten the progress to higher production averages. Asmundson (1927*a,* 1927*b,* 1928) has reported results from six years of breeding Rhode Island Reds, Barred Plymouth Rocks, and White Leghorns for improved egg production at the University of British Columbia. The results of twenty years of mass selection of high- and low-egg-production lines at the Cornell Agricultural Experiment Station have been reported by Hall (1935). Hall's conclusion that egg production has been improved by this method of selection has been challenged by Petrov (1935) who has pointed out that, with the exception of the first four years of selection, the increase in egg production seemed to be due to improved environmental conditions, since both high and low lines improved in average egg production.

During the early part of the present century, practical poultry breeders selected birds for mating largely on the bases of physical appearance and breed characters stressed by the Standard of Perfection. When trapnesting and pedigree systems came into common use, strong reliance was placed on the ancestry of the individuals mated. This was soon followed by a combined consideration of the individual's performance along with its ancestry. During this period, the poultry industry began to strive for high individual records. The production of 300-egg hens became the goal of breeders.

Recently, there has been a tendency to add progeny testing to the bases for selection of birds for breeding. This last step, introduced to the field of poultry breeding by Pearl, combines all of the information available from ancestry and individual records of performance with an actual test of the bird's breeding ability. This type of selection has also tended to change the emphasis from an individual basis of selection to a family basis. Not only good individuals, but good individuals from good families, are wanted.

From a genetic standpoint, the progeny test is based on sound principles. Many good individuals with similar phenotypes are known to be genotypically dissimilar, some being homozygous and some heterozygous for different important genes controlling production characters. A good bird from a uniformly good family is likely to be homozygous for and

breed true for a greater number of desirable genes than a good individual from a poor family. The final proof of the value of a breeding bird is, then, found in the offspring, which show the various combinations of hereditary factors that the parent can actually transmit to the next generation. This is especially so, since the actual number of genes involved in the inheritance of egg production is not known. Estimates vary from 8 pairs postulated by Hays and Sanborn (1934) to 200–300 suggested by Munro (1937). Whatever the exact number may be, the phenotypes displayed by the progeny or by the sisters of the individuals considered give a means of estimating the relative values of their genotypes.

CHARACTERS GOVERNING THE ANNUAL EGG RECORD

The annual record is a measure of the productivity of the individual and reflects the contributions of all egg-production characters. The ideal condition to strive for is the best combination of all of the desirable characters involved. The number and importance of the independent factors entering into the annual record can be adequately illustrated by actual trapnest records of some individuals. A number of birds may have the same annual record, but it may be conditioned by entirely different characters in each case. Five representative individual trapnest sheets selected to illustrate this point appear in figure 1. The five birds laid very nearly the same number of eggs in the thirteen calendar months beginning with September 1. Yet an examination of the course of egg production in these birds will show five different reasons why the figure of approximately 200 eggs in each case was not exceeded.

The bird whose record is shown in figure 1, *A*, was a late-maturing individual, not starting production until she was 305 days old. Although she laid at a high rate, the late sexual maturity limited her record for the year.

Similarly, the length of time in production of the bird in figure 1, *B*, was limited by an early molt. She evidently was a nonpersistent bird and, though fairly early-maturing and laying with reasonable intensity, did not exceed the 200-egg mark because of early cessation of production.

Figure 1, *C*, on the other hand, illustrates the loss of time in production during the laying year, rather than at its beginning or end as in the previously mentioned cases. This bird went into a pullet molt or, in other words, exhibited winter pause, during the months of December and January, which limited her possibilities of attaining a high record.

The case of the bird in figure 1, *D*, which became broody on four occasions during the year, also shows a similar loss of time in production.

Finally, figure 1, *E*, shows the record of a bird that possesses most of

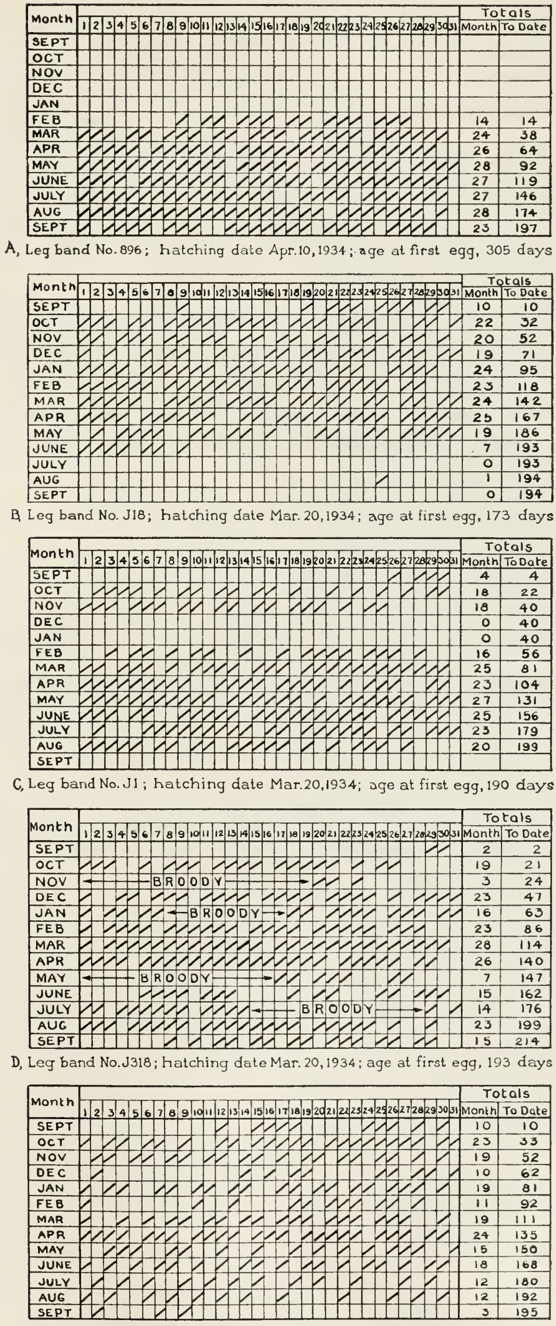

Fig. 1.—Conditions lowering the annual record: *A,* late maturity; *B,* poor persistency; *C,* winter pause; *D,* broodiness; *E,* low rate.

the desirable characters governing time in production—her maturity and persistency are satisfactory, she was nonbroody and lost very little time by winter pauses. And yet her record was as low as those of the other four. The explanation lies in her inability to lay at a high rate. While the bird in figure 1, *A* exhibited monthly production figures of 24, 26, 28, 27, 27, and so on, this bird laid only 19, 24, 15, 18, and 12 eggs respectively. Although the factors which need improvement in these five birds are different, no indication that this is the case could be obtained from the total annual egg records alone.

However, the conditions existing in reality are even more complicated. The birds in figure 1 each exhibited one principal defect. Most birds show various combinations of these defects, often two and sometimes three or more at a time. Yet it is possible both for the trapnesting breeder and the nontrapping multiplier to detect and estimate the severity of these defects in the flock.

Methods of detecting and measuring each of these defects with and without trapnesting are discussed in the following sections.

Sexual Maturity.—Sexual maturity is the character which expresses the rate of sexual development of the bird and the onset of egg production. This factor is the one that Pearl principally studied when he investigated winter production. In his stock it was the early-maturing birds which laid the most eggs before March 1 of their first laying year. When maturity is considered on a time scale, a less arbitrary criterion of this character is available. If all of the birds considered are hatched on the same date, the date of the first egg laid provides such a measure. If, however, the date of hatch is variable, maturity may more logically be measured by the age at first egg.

There is, however, a complication involved here too. Climatic conditions are known to affect the rate of growth of individuals; early-hatched chicks, as a rule, grow and develop faster than do late-hatched ones (Kempster and Parker, 1936). The age at first egg is affected by a seasonal retardation of growth, associated with high temperature. The California Station flock is usually hatched in March and April, but even in this short season, differences develop: each week's delay in hatching delays the date of first egg by 10 to 12 days, or, in other words, the average age at first egg is increased by 3 to 5 days. In a similar manner, nutrition affects the age at first egg: for example, the addition of 15 per cent wheat bran to a ration containing no bran used at the California Station lowered the average age at sexual maturity by approximately 15 days.

Artificial light is another environmental factor which may decrease both the age and the date of sexual maturity. Thus Scott and Payne

(1937), by subjecting turkeys to artificial light, accelerated the onset of production by nearly two months. Similarly, Bissonnette and Csech (1937) and also Clark, Leonard, and Bump (1937) obtained earlier eggs from pheasants by providing artificial light.

Age at first egg, however, seems to be a satisfactory criterion of sexual maturity in chickens, and with the recognition of and provision for the influence of hatching date, it can be safely used, when other management factors are uniform. In turkeys, Asmundson (1938) has found date of first egg to be superior to age at first egg as a measure of maturity.

That sexual maturity affects annual production is clearly seen from figure 2, which illustrates the effect of the date of first egg on the length

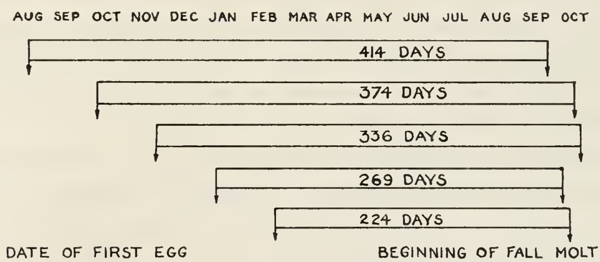

Fig. 2.—Length of laying year in relation to date of first egg. Birds are grouped according to date of first egg, in 50-day periods.

of laying year of a flock of pullets. The actual production is not shown here largely because there are inherent differences in intensity of laying between the individuals whose records were used for this chart. If equal rates of production were found in all groups, the length of time in production would be directly related to the annual record. Figure 2 indicates that birds maturing in February have only slightly more than 50 per cent as much time in production previous to the annual fall molt as birds maturing in August. The fall molt occurs at about the same date regardless of date of maturity. In commercial practice, the factor of early maturity is of added importance, for most of the birds are hatched in the spring months, and hence those that are early-maturing usually lay more eggs at the time of high egg prices.

That sexual maturity is inherited has been demonstrated definitely by Pearl (1912), by Hays (1924), and by Warren (1934). In determining this character both sex-linked and non-sex-linked genes are involved. Sex-linked inheritance in chickens operates in such a manner that the sire exerts more influence than the dams on the character observed in the daughters (see p. 4 in section, "Explanation of Terms Used in Breed-

ing"). Consequently it is of paramount importance to use sires from early-maturing families if one desires to improve his flock for this character.

Hays (1924) has suggested that two pairs of genes are involved in the inheritance of early maturity: *EE,* which is sex-linked (*E*– in females) and *E′E′*, which is not. According to Hays, either gene in the dominant state will produce early maturity, while late maturity will ensue when both are recessive. Warren (1934) has produced evidence that both *E* and *E′* are necessary for a satisfactory early maturity. The situation may be even somewhat more complicated, but in any case, at least two pairs of genes are involved, one of which is sex-linked.

There is a possibility of having birds which mature too early. Precocious maturity is associated with small body size, which is one of the factors contributing to small egg size (see section entitled "Egg Size," p. 24). Precaution must therefore be taken to guard against developing too early maturity as well as against too late maturity.

Hays (1936*a*) has produced evidence that the earliest phenotypic group of Rhode Island Reds mature at less than 180 days of age. These birds were assumed to carry genes *E* and *E′*, since they produced offspring maturing on the average earlier than the offspring of dams maturing at 180 days or more. The border line between early maturity and precocity has not yet been determined. However, general breeding experience would indicate that birds maturing at less than 150 days of age are apt to be small and to produce small eggs. Furthermore, at least in one case on record (Knox, 1930), such birds did not produce as many eggs as the birds maturing at between 160 and 210 days of age.

Identification of both early- and late-maturing birds is accomplished very easily. The trapnest record, of course, is the best guide, but physical selection of early-maturing birds is relatively simple. Any culling guide gives directions for selecting early-maturing birds.[5] The late-maturing birds should be marked in order to eliminate them from any future use as breeders. They may, however, still prove to be fairly profitable egg producers, if they are healthy and of average size.

[5] Most general texts on poultry contain instructions for culling, for example:

Jull, M. A. Poultry husbandry. 2d ed. *viii* + 548 p. Illus. McGraw-Hill Book Company, Inc., New York, N. Y. 1938.

Lippincott, W. A., and L. E. Card. Poultry production. 723 p. Illus. Lea and Febiger, Philadelphia. 1934.

There are also books dealing specifically with the subject of culling methods:

Rice, J. E., G. O. Hall, and D. R. Marble. Judging poultry for production. *xii* + 425 p. Illus. John Wiley and Sons, New York, N. Y. 1930.

Payne, L. F., and H. M. Scott. International poultry guide for flock selection. 142 p. Illus. International Baby Chick Association, Kansas City, Mo. 1934.

Pauses.—Pauses occurring in the production record between the time of the first egg laid and the normal fall molt may be broadly classified into three groups: winter pause, pause due to broodiness, and spring and summer pause.

Winter Pause: One very important problem in connection with pauses in the winter as well as those in the spring and summer is the debatable question as to what constitutes a pause. At various times, different workers on the subject have used some given number of successive days of nonlaying for a definition of pause, the number of such consecutive days varying from 4 to 15. As yet no clear-cut definition, which would not be arbitrary, has been suggested, the major difficulty being the fact that the underlying reasons for such pauses are not well understood. In many cases, pauses can be recognized in the individuals of a flock by head, neck, or body molt. As has long been recognized, birds going out of production usually start molting. Often the severity of the molt—which is judged by knowledge of the order of the normal molt (head-neck; breast-abdomen-back; wings; tail)—serves to indicate the length of the pause. The winter-pause molt is usually confined to the head and neck. Some individuals, however, lay through a molt, and others pause for a short period of time without molting. In a trap-nested flock, all types of pausing birds can be accurately recognized, but in a flock which is not being trapped, some are improperly classified even by those well trained in the use of known physical methods of culling.

Little is known about the factors involved in winter pausing. That pauses are brought on by environmental factors in many cases is well recognized, for sudden changes in management, extremely rough handling, and sudden climatic changes often result in pause. Since earlier-hatched groups of pullets of the same strain regularly show a greater amount of pause than later-hatched lots, there is probably a direct relation between age of the bird and the internal conditions which cause her to cease egg production. Yet at the same time that some birds in any flock of a given age show a pause, others may go through such disturbances and continue to lay. This gives evidence that there are differences between birds in their thresholds of response to conditions producing a pause. Evidence from the California Station flock indicates that such differences are, at least in part, hereditary. If such is the case, the possibility of selection and breeding for absence of pause immediately presents itself.

That such procedure is wise can be illustrated by the losses a poultryman sustains by having many pausing birds in his flock. Thus, some years ago in the California Station flock, birds showing a pause of 7 or more

days were found to lay on the average about 56 eggs during the four winter months (November through February), while the nonpausing birds during the same time laid on the average 77 eggs; the winter production of the nonpausing birds was over one-third greater.

Hays (1924) has postulated that the inheritance of winter pause depends on a dominant gene *M* for its expression. Thus, birds of the constitution *mm* would be free from pause. However, the mode of inheritance of the factors responsible for the occurrence of winter pauses is not so simple as this, for, if it were, the elimination of pause from a flock would be easily obtained by breeding only from nonpausing (*mm*) families. At present, the best a breeder or multiplier can do is to select for mating those families or individuals which show greatest freedom from pause. For breeding selection against pause, pullets which are from 7 to 8 months of age in November will probably give a better differentiation between genetic pausers and nonpausers than either older or younger birds. The trapnest breeder can base his selection on periods of nonproduction in the egg records. In the nontrapnested flock, reliance must be placed on the appearance of molt in birds. Although some of the pausing birds may prove profitable egg producers, they should be identified so as to be eliminated from the breeding flock.

Broodiness: This type of pause is of greater importance in some breeds than in others. The Asiatic breeds are very broody as a rule. The American breeds, such as Plymouth Rocks, Rhode Island Reds, and Wyandottes, are subject to considerable broodiness, while most of the Mediterranean breeds seem to be comparatively free from it; but no strain of any breed has ever been reported to be completely nonbroody. Selection against broodiness should be very rigorous, since if unchecked it may become an important problem, especially in small breeding flocks.

Of the different characters involved in egg production, broodiness is one upon which considerable genetic and physiological data have been obtained. Two pairs of dominant complementary genes, *A* and *C*, seem to be involved in producing broodiness, according to Goodale, Sanborn, and White (1920). The presence of either *A* or *C* alone will produce no effect, but the two brought into combination will result in a broody bird. Thus two nonbroody lines crossed together may produce broody progeny, if one of the lines possesses the factor complementary to the one carried by the other line. For instance, a cross between *AAcc* and *aaCC* will result in a broody bird, *AaCc,* heterozygous for both genes. In the Cornish breed, Roberts and Card (1934) have obtained evidence of an additional sex-linked gene for broodiness.

A situation involving complementary genes makes it difficult for any

breeder to eliminate broodiness completely from a strain. The incidence of broodiness may be greatly reduced, however, by a method of testing the genotype of breeding birds. This method involves the isolation of two nonbroody strains: one carrying gene A without gene C, the other carrying C without A. When crossed, these strains produce broody daughters. Prospective breeding males and females can be mated to first one and then the other of the test strains. If no broody daughters are produced from the mating with either strain, then the prospective breeding bird carries no genes for broodiness and is of the constitution *aacc*.

In a flock where such a program is not feasible, elimination of the broody families or, in the case of nontrapnested birds, of broody individuals from the breeding flock, should be made. Since broodiness is a very conspicuous character, this plan can easily be carried out. In the simplest form it involves placing a colored legband on a bird that at any time was taken off the nest as being broody. Once identified, such birds can be disposed of in any manner desired.

The importance of broodiness in the annual record of a bird depends both on the number of times during the year that a bird becomes broody and on the length of time before the bird resumes laying. Both of these factors are extremely variable; the latter is in part dependent on management, since the sooner a broody bird is detected and prevented from sitting, the more quickly she will return to production.

The physiological basis of broodiness is better understood than that of most of the other characters discussed. Broodiness is produced by prolactin, a hormone secreted by the anterior pituitary body. This is the same substance that controls the production of crop milk in pigeons as well as of the milk of nursing mammals (Riddle, Bates and Lahr, 1935). Byerly and Burrows (1936) have found that broody females and males from broody strains produce more of this hormone than nonbroody birds.

Spring and Summer Pauses: Besides the pauses occurring in the winter months and pauses due to broodiness, there are other periods of interruption of egg production, which may appear during the spring or summer. Superficially they seem to be of the same nature as the winter pauses, but actually they have been demonstrated (Lerner and Taylor, 1936) to be the result of other causes which have not as yet been determined. Whether hereditary factors are concerned in the production of these pauses is not known at present, consequently neither is it known whether or not selection against them is feasible. Superior birds, however, do not exhibit this condition, so that discriminating against spring and summer pausers in a breeding flock is a safe policy because of the possibility that this defect may be transmitted to their progeny.

Persistency.—The character limiting or extending egg production at the end of the laying period is known as "persistency"; the cessation of production is usually accompanied by the onset of the annual (fall) molt. Its importance, recognized by Rice (1914) before the development of the Goodale-Hays hypothesis, can be readily demonstrated in the same manner as that of early maturity. Thus figure 3, based on the same stock as used for figure 2, shows that the early-molting birds have a much shorter period of lay than the late molters. Thus the birds molting in June were in production about 60 per cent as long as those molting in December. Figure 3, like figure 2, indicates that there is no relation between date of first egg and the time of onset of fall molt.

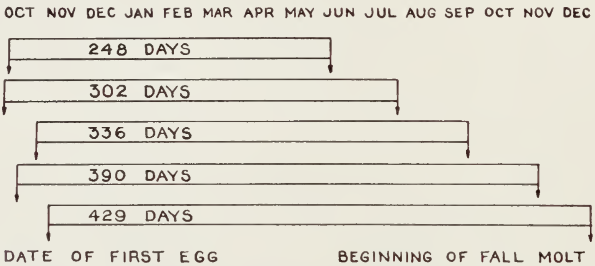

Fig. 3.—Length of laying year in relation to beginning of annual molt. Birds are grouped according to date of molt, in 50-day periods.

A rather important question in connection with persistency is the selection of an adequate method of measurement. There is a large number of these available, the most prominent ones being the length of biological laying year, suggested by Hays and Sanborn (1926); production in August and September, used by Knox, Jull, and Quinn (1935); and age at last egg or date at last egg, originally mentioned by Goodale (1918) and recently brought back to usage by Lerner and Taylor (1937*a*). The latter measures are deemed more adequate than that of Hays and Sanborn on the grounds that length of biological laying year depends on sexual maturity as much as on persistency and hence is not a true measure of the latter (Lerner and Taylor, 1937*b*). In view of the above criticism of the use of the biological laying year as a measure of persistency, Hays's (1936*b*) claim that persistent production results from the action of a single dominant gene *P* should be submitted to further experimental test. The measurement used by Knox, Jull, and Quinn reflects the inherent rate of production as well as the ability of the bird to lay late in the fall, and thus also fails to give an uncomplicated measurement of persistency.

As far as the preference between age at or date of last egg is concerned, there seems to be a greater effect of date of hatch on the age at last egg than on date at last egg. Both can be demonstrated to be inherited to an equal extent, when a population hatched during a limited season is considered. By analogy with sexual maturity, the age measure may be used in preference to the date measure, especially if correction for hatching date is made. Probably breeders hatching stock over a period of several months will find it easier to use the date of last egg as a measure of persistency. In turkeys, Asmundson (1938) has used this measure as an adequate criterion of persistency.

Whichever method is used, selection by the breeder can be readily practiced for this character. Such selection, if properly carried out, should be effective in increasing the length of time the flock is in lay, but caution must be exercised, just as in the case of early maturity, not to overdo it.

In commercial practice, a flock of yearling hens which will lay through the late fall at the time of the highest egg prices will be highly profitable. A breeding flock, on the other hand, if in lay at a late date, may not return to full production after the molt by the time hatching eggs are desired. A practice of forced molting might be necessary in highly persistent breeding flocks, but it would tend to nullify any attempt to select for extreme persistency. In order to make possible adequate selection of birds for persistency, forced molting probably should not be started before the end of September.

Rate of Production.—The factor of intensity, or rate of production, is also one for which a number of measurements have been proposed. The most common way of representing rate is by the use of percentage production. This may be designated as *gross rate* and has the distinct disadvantage of permitting confusion of nonpausing birds possessing low intensity with birds which show pause but have a high rate of production when in lay. Since some types of pause are inherited independently from rate, they should be measured separately. The *net rate* of production accomplishes this by eliminating pausing days from consideration. Thus, instead of dividing the number of eggs laid in the period considered by the total number of days involved, it is divided by the latter number less the days broody and in pause. The difficulty arising here is again the one of deciding just what constitutes a pause. Until more information on the subject is available, only arbitrary standards can be used. In some of the work carried out at this station, where 7 days has been used as a minimum standard for pause, the comparative figures in table 1 were obtained.

As may be seen, the winter pauses are distinct from rate, since the net

winter rate is almost the same irrespective of whether the birds paused in the winter. The gross rate in the two cases, however, is different, the winter-pausing birds falling about 20 per cent lower than the nonpausing birds. Spring and summer pauses, however, seem to have a somewhat depressing effect on rate, this being one of the points of evidence for a distinction between them and the winter pause. The main point these data illustrate, however, is that the gross rate may be a misleading criterion of measurement of the inherent intensity of production.

Average clutch size has been used by Hays and Sanborn (1932) as a measure of intensity. It is, however, somewhat more laborious to calculate and, furthermore, does not reflect the number of nonlaying days between clutches of eggs, which should enter intrinsically into the calculation of rate. A hen laying an egg each third day would have the same average clutch size as a bird laying an egg every other day, but the latter would have the higher net rate. The suggestion of Hays and Sanborn (1934) that two dominant genes I and I' determine clutch size does not necessarily solve the problem of inheritance of rate of production, particularly because of the arbitrary assignment of clutch sizes to specific genotypes.

TABLE 1

GROSS AND NET RATES OF PRODUCTION FOR PAUSING AND NONPAUSING HENS*

	Winter rate		Spring rate	
	Gross	Net	Gross	Net
	per cent	*per cent*	*per cent*	*per cent*
Winter-pausing birds	46	65	74	77
Spring- and summer-pausing birds	63	64	58	70
Birds pausing both winter and spring or summer	47	64	56	71
Nonpausing birds	65	67	74	75

* From Lerner and Taylor (1936).

In using net rate, one should choose a short period, rather than the whole year. This is largely because the average annual rate may also lead one to an erroneous evaluation of the inherent intensity of a bird. Thus, a bird pausing during the winter months will have undue weight laid on her spring production, which is normally higher than the winter production; and a nonpausing bird will be penalized by the inclusion of her winter record in the calculation of her rate. Since, however, rates at different periods of the year bear a definite relation to each other, a shorter period of evaluation can be used with a fair degree of precision. In general, the rate during the spring months (March to June) is found to give a higher correlation with the annual egg record than does the

winter or the summer and fall rates; but the correlation between winter rate and annual production is sufficiently high to make it feasible to rely upon winter rate. This has the additional advantage that, outside of the birds which pause through most of the winter months, an evaluation of the inherent rate can be thus made in pullets before the breeding season.

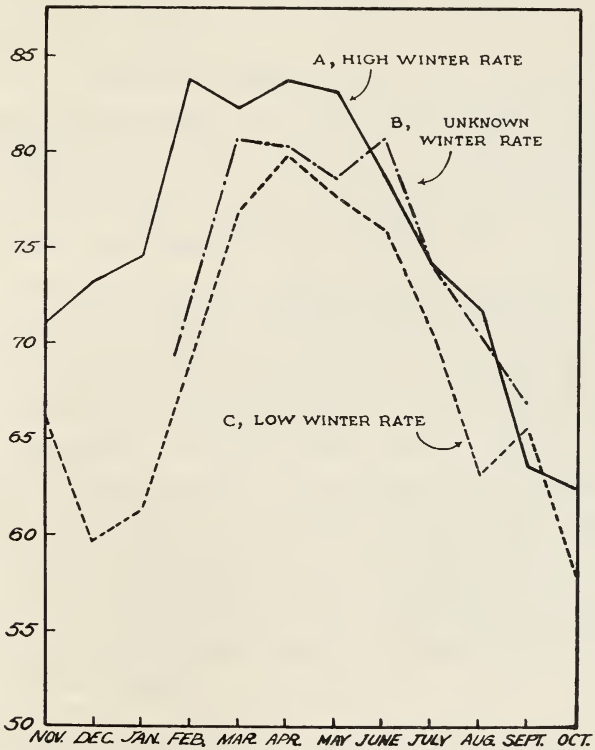

Fig. 4.—Relation of fall and winter rate to annual rate: *A*, birds laying 21 or more eggs in each of any two of the winter months (November, December, January); *C*, birds laying less than 21 eggs in two of these months; *B*, birds, information on which is lacking for these months.

Figure 4 illustrates the fair degree of accuracy obtained by such a method of classification with nonpausing birds. An arbitrary standard of 21 eggs a month in any two of the three winter months (November, December, January) is used for high rate. Birds fulfilling such a requirement exhibit on the average a higher rate of lay throughout the rest of the year than those falling below it. The third curve on the graph represents the production of birds which either paused during the winter months or were extremely late-maturing. Birds with both low and high

rates were present in this group, since the average production is found to be intermediate between the other groups. The rate of such birds would have to be judged by their performance in the spring. Since, however, these birds would in all likelihood not be bred from, because they exhibited a winter pause or exceedingly late maturity, no disadvantage in delaying the collection of information on the rate of such birds is incurred. In all groups, the highest rate of production occurred from March to May, and the differences in rate between high- and low-rate groups were least in the spring and summer months.

The above methods of identifying birds possessing high or low rate are obviously suitable only for trapnested flocks. Unfortunately, there are no precise physical criteria by which rate can be judged, so that individual selection is impossible in nontrapped flocks. A short trapnesting period will achieve the desired ends; otherwise only pen selection is possible. Where pause is not a significant factor, percentage production of one pen as measured against another may serve a useful purpose.

General Considerations of Production Characters.—The general discussion of the genetic factors affecting egg production in relation to practices of selection can now be summarized. Some of the characters controlling time in production, such as maturity, persistency, and broodiness, are inherited on a basis such as to make selection for the desirable genes possible. The trapnester should have no difficulty in interpreting his records on these characters and in setting up standards of selection. Further, where trapnesting is not practiced, certain physical manifestations of maturity, persistency, and broodiness are easily observed; and most culling guides provide complete instructions for the recognition both of superior individuals and of those to be eliminated from the breeding flock.

Manifestations of pauses are not so readily interpreted. While neck molt is a fair criterion of the expression of the winter-pause character, there is considerable difficulty in setting up satisfactory and efficient standards of selection in these cases. This applies less to the trapnesting breeder than to the nontrapnesting multiplier.

The condition of summer pause is still more difficult to interpret, since it shows some association with low rate, and rate is the hardest character to measure unless some trapnesting is practiced. If at least part-time trapnesting is practiced, selection for high rate is feasible. Otherwise, little reliability can be placed on the use of physical standards of selection, and improvement of the inherent intensity of production in a flock is beset with great difficulties.

The best birds are not the ones which are superior in only one par-

ticular character, but those which exhibit the best combination of all of the characters considered. The annual record and the monthly and seasonal distribution of egg production throughout the year are in the final analysis the main criteria of the profitableness of a bird's production. Their expression is conditioned by the combination of the characters discussed; hence, the latter should always be considered, not only singly, but also in relation to each other and to their contribution to the annual record.

When flock efficiency is considered, however, a whole new series of characters, some of which are undoubtedly inherited, comes into the picture. These are the characters affecting the viability of birds. Flock efficiency will, of course, be lowered if mortality is high. Selection for resistance to adverse environmental conditions or for the ability of the bird to live must, therefore, now be considered.

CHARACTERS AFFECTING VIABILITY

The influence of the conditions affecting viability on the efficiency of production of the flock begins with the egg and continues throughout the productive life of the bird. The number of chicks hatched from a given number of eggs, the proportion of these raised to maturity, and finally the mortality of the laying birds, all have an effect on the size of the flock and on its productivity. Just how much of the embryonic and post-embryonic mortality is due to inherited factors cannot be estimated accurately, but there is good evidence in many cases that at least part of the mortality up to the completion of the first laying year is controlled by genetic factors, and hence the condition is amenable to improvement by proper breeding methods.

The mortality most closely related to egg production is that occurring during the first laying year. This is evidenced by reports available on commercial flocks where as high as 100 per cent replacement has been necessary during the first laying year. The replacements are not entirely due to mortality, since some of the birds removed, though nonproductive, appear anatomically normal, and others are unprofitable because of nonfatal pathological conditions. However, at least half of the replacement in an average well-cared-for flock is likely to result from actual deaths from nonspecific pathological conditions, that is, conditions not related to definite infectious or dietary factors. This point was brought out by Lubbehusen and Beach (1938) in an analysis of mortality in the California Station flock.

The presence of birds that are doomed to die during the laying year and also of birds which fail to lay because of specific diseases causes a

flock to be less profitable. To illustrate this point, limited evidence on the California Station flock indicates that birds which succumb to paralysis and associated conditions in the spring months show a reduced production during the previous fall months although they appear normal in every other respect. In a similar manner Asmundson and Biely (1930), among others, have reported that adult carriers of pullorum disease show a reduction in egg production. On the other hand, we have evidence that birds developing disturbances of the reproductive system seem to lay normally up to the time of onset of the outward manifestations of the condition.

In any case, if any of the various diseases to which poultry is subject have a specific hereditary basis of susceptibility or are conditioned even in part by a general constitutional weakness, breeding methods may be of value in increasing the flock efficiency by the creation of lines more resistant toward such conditions.

Longevity.—Partly on these grounds, Pearl (1923) suggested breeding from aged birds only. He believed that the productivity of the breeding birds would be improved along with longevity. Greenwood (1932), however, has found that very old birds showed no marked superiority in offspring, while their progeny was limited in numbers by low fertility and hatchability. Whether or not such is the case, greater viability will ensue in a flock as a consequence of selection of longer-lived strains. Differences in mortality between families in the same flock are known to persist for several generations, as they have in the California Station flock, and hence are probably heritable. Despite the poultryman's interest in obtaining long-lived birds, comparatively few reports are available on the results of selection for longevity. This fact may indicate that breeding for characters influencing longevity is a complex process.

Disease Resistance.—Some experimental evidence of the inheritance of resistance to specific infections in chickens has been obtained. Roberts and Card (1926 and 1936) have demonstrated inherited differences in susceptibility to pullorum disease, and Lambert and Knox (1932) obtained similar results with fowl typhoid. They failed, however, to obtain strains in which all the birds were resistant. Furthermore, such diseases can be more efficiently controlled by other means. On the other hand, there is evidence on the hereditary nature of resistance to certain other disease conditions for which methods of prevention and control are not yet known. This applies particularly to neurolymphomatosis (paralysis) and may also be true of other forms of lymphomatosis (big-liver disease or leukemia), leucosis, and certain types of tumors.

Present conceptions of the nature of such pathological conditions are

conflicting, but there is considerable experimental and statistical data from British Columbia (Asmundson and Biely, 1932), Louisiana (Upp and Tower, 1936), Idaho (Gildow, Williams, and Lampman, 1936), Iowa (Wilcke, Lee, and Murray, 1938) and from the California Station flock, to indicate the existence of definite differences in degree of occurrence of this group of diseases between different families. These data point to the possibility of partial control by selective breeding. Results obtained with the California Station flock having a bearing on this problem are discussed in a later section (p. 43).

A suitable method of selection against these diseases in an affected flock involves breeding from families which are as free as possible from paralysis and other neoplasms, rather than the selection of survivors from susceptible families. Since the genetic nature of disease resistance is usually fairly complicated, the latter method would result in perpetuation of factors for susceptibility in the flock. The former method, on the other hand, would tend to eliminate any family of birds which shows an undue concentration of such undesirable factors.

All available evidence indicates that disease resistance is specific in nature. Creating a strain resistant to one disease does not mean that the strain will be resistant to any other disease. Nor does it mean that the strain will be unusually susceptible to some other disease. Genetically, every disease presents a separate problem of breeding for resistance. Whether or not genetics can be effectively applied to the control of all diseases is questionable. Those for which specific control measures have been developed can undoubtedly be handled more easily by such means, rather than by breeding. Extension Circular 8[6] should be consulted for other more direct methods of control of diseases.

METHODS OF MEASURING FLOCK PRODUCTION

Several ways of expressing the average egg production of a flock have been commonly used. The least-accurate method is that of the *average of the records of surviving birds*. A better method involves the computation of *hen-day averages*. This method is well suited for cost-account work, since the denominator represents the average number of birds in the flock for a given period of time.

A measure of breeding-flock values known as the *production index* has been developed at the Kimber Poultry Breeding Farm. This measure is the quotient of the number of eggs laid by the group under consideration (family, flock, etc.) over the original number of pullets in the group. Any

[6] Beach, J. R., and S. B. Freeborn. Diseases and parasites of poultry in California. California Agr. Ext. Cir. 8:1–110. 5th ed. 1936.

birds that die at any time during the laying year are thus considered equally with the survivors as members of the flock or family. In that manner, a flock or family exhibiting high mortality will be penalized. Just as the annual egg record reflects all the various characters influencing the egg production of an individual bird, the production index expresses them for a group of birds. While neither the productivity nor viability of a family is reflected separately in the production index, this index gives a true picture of the interaction of all of the factors involved. To obtain measurements on the individual characters contributing to production, one has to resort to the separate determination of all of the variables previously discussed.

The production index is superior to both the average of the survivors and the hen-day average as a measure of the productive efficiency of breeding flocks. The average of the survivors completely ignores the important factor of mortality in the flock; the hen-day average fluctuates greatly with the use of various culling practices, so that a heavily culled flock may show a better average production than an unculled flock of the same inherent productivity. Both mortality and culling decrease the average egg production expressed as a production index, which thereby shows the prevalence of nonproductive or nonviable birds in the flock.

CHARACTERS GOVERNING THE QUALITY OF EGGS

All of the discussion to this point has referred to the quantity of production. Factors affecting quality of production may be discussed next.

Egg Size.—Probably the most important character concerned in the quality of commercial eggs is that of size. The production of large eggs within a reasonable period of time after sexual maturity is now recognized as an essential in a good egg-production strain. Rigid selection in breeding flocks has brought about during the last fifteen years a remarkable improvement in the size of egg produced by many strains.

That there is a direct correlation between body size and egg size, within a breed or within a strain, has long been known. Very small birds rarely produce large eggs. Table 2 illustrates the relation between body weight and egg weight. The 595 birds involved were weighed in December, and the December and January egg weights were calculated for birds at different body weights. Sexually mature pullets which are still growing will improve their egg size as they become larger.

Seasonal effects expressed through temperature also affect egg size: Lorenz and Almquist (1936) have shown an average decrease of 1 ounce per dozen in mature birds for each 30° F increase in maximum daily temperature.

Rate also may be related to egg size, producers of very small eggs often having a phenomenal rate, while producers of exceptionally large eggs seldom have a high rate. This relation is illustrated in table 3. However, this does not mean that all birds laying small eggs have a high rate of production. Since egg size is the result of the sum of the weights of the various parts of the egg, any circumstance reducing the weight of a com-

TABLE 2

RELATION BETWEEN BODY WEIGHT AND EGG WEIGHT IN 595 WHITE LEGHORN PULLETS

Body weight at 8 months of age	Class average	Number of birds	Average egg weight in December and January*
grams	*pounds*		*ounces*
1,100-1,399	2.76	8	1.621
1,400-1,699	3.42	236	1.781
1,700-1,999	4.08	272	1.900
2,000-2,299	4.74	75	1.975
2,300-2,599	5.40	4	2.000

* From 8 to 10 months of age.

TABLE 3

RELATION BETWEEN WINTER RATE OF PRODUCTION AND EGG WEIGHT IN 145 WHITE LEGHORN PULLETS

Number of birds	Net winter rate (November-February inclusive)	Winter egg weight (November-February inclusive)
	per cent	*ounces*
14	56.0–63.9	1.852
44	64.0–71.9	1.855
69	72.0–79.9	1.841
18	80.0–87.9	1.810

ponent part reduces egg size. Thus, Buckner, Martin, and Insko (1930) have shown that a deficiency of calcium in the diet reduces the amount of shell per egg and also results in smaller egg size.

From a breeding standpoint, the most satisfactory short period in which to determine the egg size of individuals is during the late winter or early spring or, more specifically, in California during February and March. By that time, pullets hatched in the previous breeding season are approximately one year old, have reached adult body size, and produce eggs under a moderate range of temperatures in most areas in California. Egg size during this period is also reasonably close to the average size of egg produced during the pullet year of production, as can be seen from

table 4. Comparative inherent egg size can be determined at any season, but the early spring period is least subject to adverse environmental influences. Where greater accuracy is desired, about 5 eggs a month may be weighed. Weighing every egg scarcely adds sufficient accuracy to warrant the labor involved.

Hays (1929, 1937) has advanced a hypothesis for the inheritance of egg size involving a dominant gene *A* producing small eggs and dominant genes *B* and *C* for large eggs. When *A, B,* and *C* are present, an intermediate, but predominantly small size of egg is obtained. According to this hypothesis, the genotypic constitution for largest egg size should be *aaBBCC,* which would represent a pure-breeding large-egg type. Rigid selection of both male and female breeders for egg size should act to eliminate the undesirable *A* genes rather rapidly, and cause *B* and *C* genes to become homozygous at the same time in an increasingly large portion of the flock. While Hays' data lend considerable support to this hypothesis, it is questionable whether or not the gene combinations suggested by him have universal application. One practical difficulty in flock breeding lies in the fact that the contribution of the male for all egg characters can be determined accurately only by progeny tests. Practicing rigid selection of breeding males on the basis of egg size exhibited by their female ancestors or their sisters is, however, fully as important as selecting females with large egg size for mating.

TABLE 4

Monthly Variation in Egg Weight in a Flock of 116 White Leghorn Pullets

Month	Average egg weight	Month	Average egg weight
	ounces		*ounces*
November	1.753	June	1.997
December	1.834	July	1.997
January	1.926	August	2.021
February	1.965	September	2.067
March	1.972	October	2.081
April	1.972		
May	1.961	Annual average	1.962

The discrimination against small eggs on the market is sufficient to encourage the production of large eggs. However, egg size may be selected to the point where it becomes undesirably large. Minorca varieties frequently produce eggs averaging 30 or more ounces per dozen. These eggs are too large for the standard types of fillers and cases used for chicken eggs. Occasional premiums for "jumbo" sizes may influence some poultrymen to attempt commercial production of this type of egg. The

low hatchability associated with extremely large eggs (Dunn, 1922), however, should be sufficient argument against breeding for this size. Better hatchability results are usually obtained by selecting for breeders hens with average egg size ranging from 24 to 28 ounces per dozen.

Egg Shape.—There are three common shapes of eggs: long, ovoid (typically egg-shaped), and round. Long types are not commercially desirable since the fillers of egg cases are not deep enough to take a large long egg. Similarly, large round eggs are too wide for the ordinary filler. From a hatchability standpoint, furthermore, ovoid eggs in common experience give better average results than either very long (Landauer, 1937) or round types.

The inheritance of egg shapes is not clearly understood. Benjamin (1920) states that long-shaped types are dominant over normal types, but Kopeć (1924) has presented contrary evidence. Some casual observations made by the senior author would lead us to believe that round may be dominant to ovoid. Axelsson (1936), however, has found no dominance of any one shape over another in several breed crosses. Rigid selection for ovoid types tends to bring rapid improvement in the character of the eggs produced by the flock. It is important that the breeding males come from families producing ovoid-shaped eggs.

Many types of misshapen eggs seem to be produced by temporary or chronic inflammation of the shell gland of the oviduct and are probably not inherited. Unless the breeding hens displaying such conditions have proved to be valuable breeders, such birds should probably be removed from the breeding flock. Misshapen eggs show notoriously poor hatchability.

Egg Color.—In the common breeds of chicken, egg color is usually some shade of either brown or white. One peculiar breed, the Araucana, lays a blue egg. Breeds of the Mediterranean class, such as Leghorns, Minorcas, and Ancona, should lay a pure-white egg. Breeds of the Asiatic and American classes should produce a brown egg. In these breeds a uniform, medium-brown color is desired. Pale-brown or creamy colors should be discriminated against.

The New York market has long been noted for its premium on pure-white-shelled eggs, while the Boston market has similarly placed a premium on brown-shelled eggs. In recent years these premiums have been lower than previously. However, in choosing a breed or strain for commercial egg production, local market preferences for egg color must still be considered.

Birds producing brown-shelled eggs and also individuals from white-shelled varieties which produce tinted or creamy eggs characteristically

show a decreasing intensity of color with advancing production (Benjamin, 1920). Immediately after sexual maturity or after any period of nonproduction, the color of the shell tends to be deeper in shade than after long periods of production. Where tints and creaminess are to be selected against, it is important to take records of color when the bird first begins to lay and after pauses and the annual molt.

Egg color is apparently controlled by several pairs of genes (Hays, 1937), some of them acting cumulatively to produce darker shades, others acting as inhibitors of color (Punnett, 1923). Crosses of dark brown by white strains usually produce eggs ranging in the medium-brown shades. Crosses of medium brown by white strains may produce fowls with egg color ranging from creamy to light brown. Blue color is dominant to white; crosses of blue and brown produce a greenish color, as Punnett (1933) has shown.

In white-egg strains, several generations of selection of both male and female breeders from white-egg families will reduce the incidence of creamy or tinted eggs to a very low proportion. Frequently, crossing two different white-egg strains produces a considerable degree of color in the egg of the offspring. Similarly, mating creamy or tinted individuals together may actually produce some birds laying brown eggs. All of these results are explained by the fact that there is probably some complementary action between some of the genes producing brown color in eggshells.

Shell Quality.—The most fundamental of the factors of shell quality is that of thickness. Thick shells are desired both for market eggs and for hatching eggs. In the incubation of eggs, characteristic differences in hatchability between matings can sometimes be traced to the amount of shell present.

Data from several generations of selection for shell thickness in White Leghorns at the California Station are given in table 5. In this experiment, birds from families selected for thick shell had a significantly higher percentage of shell during four generations than corresponding pullets bred from thin-shell lines. In these instances, the birds from both lines received the same rations and management. This evidence confirms the previous finding of Taylor and Martin (1928) that shell thickness is in part dependent upon hereditary factors. Munro (1938) has also found similar evidence for inheritance of the amount of ash in the shells of eggs from a flock of Barred Plymouth Rocks. Probably the genetic basis for inheritance of an ability to produce thick-shelled eggs is complex. The importance of nutritional factors in producing shells of high quality must also be emphasized, since deficiencies of calcium or vitamin D in the diet quickly lead to production of defective shells.

Other common types of poor shell quality are sometimes produced by closely related individuals, and the inheritance of tendencies for their production may be suspected (Hays, 1937). Such types include rough or "sandy" shells, mottled shells, and "glassy," or very nonporous shells. Hens producing these types of defective shells should be removed from the breeding flock.

Another quality which seems to be inherited is the character of the bloom or finish of the shell. While the Leghorn breed is said to produce a chalk-white egg characteristically, many individual hens lay eggs having a pronounced glossy finish. Data on the California Station Leghorn flock would indicate that a single gene difference is usually found, the chalky finish being dominant.

TABLE 5

PROPORTION OF SHELL AND HATCHABILITY IN EGGS FROM THICK- AND THIN-SHELL LINES

Year of hatch	Line	Number of pullets	Average proportion of shell	Hatchability of fertile eggs
			per cent	*per cent*
1934	Thick shell	38	9.84	82.1
	Thin shell	27	9.44	58.5
1935	Thick shell	36	9.94	90.3
	Thin shell	27	9.24	76.2

Albumen Quality.—Holst and Almquist (1931) have produced evidence that individual hens were surprisingly constant in the proportion of total albumen found to be in the firm condition. Since then, other reports (Lorenz, Taylor, and Almquist, 1934; Knox and Godfrey, 1934) have given evidence for the inheritance of this character. From further breeding results, the amount of firm white now seems to be the result of the expression of a considerable number of genes; crosses between high and low lines give intermediate results. Strains producing eggs with characteristically large quantities of firm white can be created by breeding. All experiments designed to modify the proportion of the firm white of freshly laid eggs by nutritional or other means have failed.

Van Wagenen and Hall (1936) use a different criterion of albumen quality: they make a visual comparison of the appearance of the albumen with a photograph of eggs classified according to quality. This measure, known as the *albumen-condition score,* is intimately correlated with the actual height of the firm albumen observed in egg contents removed from the shell and membranes. On the other hand, there is considerable evi-

dence to show that the *percentage-firm-white* and *albumen-height* measures are not necessarily closely correlated in eggs from certain hens. A good albumen-condition score is probably dependent upon many genes for its expression.

Good quality is required of a high-grade market egg. Lorenz and Almquist (1935) found that eggs with an original high percentage of firm white are not only of superior quality when fresh but also after storage since the rate of liquefaction of the albumen in such eggs is lower than in eggs with lower percentages of firm white. Hall and Van Wagenen (1936) have also claimed higher hatchability for eggs with the best albumen-condition scores. Some tests conducted at the California Station have not confirmed this. There seems to be no association between the percentage of firm white and hatchability.

Hatchability.—In our experience, the greatest differences found in hatchability in commercial poultry flocks have been produced by nutritional factors. Insufficient amounts of one or several vitamins and mineral substances in the rations of breeding birds frequently cause poor hatchability under practical conditions of poultry breeding. In order to obtain high hatchability as well as chicks of good quality, the breeding ration must not be deficient in these essential nutrients.[7]

Under good conditions of nutrition and management, variation in hatchability between matings is common. Hays and Sanborn (1924) have postulated a genetic explanation by which a single gene controls hatchability: *HH* individuals hatch 85 per cent or more of fertile eggs, *Hh* 55 to 84 per cent, *hh* less than 55 per cent. Jull (1932) has produced evidence which would indicate a more complex inheritance of hatchability. His view is supported by the fact that some six or more lethal genes are known to cause embryonic death in chickens. Practically, however, Hays' method of selecting birds hatching 85 per cent or more is an effective means of selecting inherently high-hatching stock; at the same time, it allows for a reasonable amount of embryonic deaths produced by noninherited conditions.

BREEDING SYSTEMS

The comparative value of various systems of breeding, by which improvements of characters in poultry have been made, has long been a subject of debate by poultry breeders. The principal systems which have been used involve close inbreeding, line breeding, outbreeding, crossbreeding, and grading.

[7] Almquist, H. J., T. H. Jukes, and W. E. Newlon. Feeding chickens. California Agr. Ext. Cir. 108:1–38. 1938.

Close Inbreeding and Line Breeding.—Some degree of inbreeding is involved when any mated pair of birds have a common ancestor. The closer the common ancestor is to the individuals mated and the greater the number of common ancestors, the greater the degree of inbreeding. Closest inbreeding is attained by successive generations of full brother to sister matings. High degrees of inbreeding can also result from mating a larger number of generations of less closely related individuals, such as are involved in half brother by half sister, father by daughter, mother by son, and cousin by cousin matings.

Numerous reports of the detrimental effects of close inbreeding are available. Four or five generations of full brother by sister matings have generally given reduced hatchability, decreased viability of chicks and adult stock, decreased growth rates, and poorer average egg production (Cole and Halpin, 1922; Dunn, 1923; Hays, 1924; Dunkerly, 1930; Jull, 1933*a*). When less-intense inbreeding, involving the mating of more distantly related birds, has been practiced, high degrees of inbreeding have been obtained with fewer detrimental effects in some instances (Jull, 1933*a;* Waters and Lambert, 1936). The latter procedure may permit more rigorous selection against undesirable genes, which often seem to be recessive and lethal or semilethal in action. Under intensive inbreeding, such genes become homozygous very rapidly in a considerable proportion of the progeny and lead to serious detrimental effects. A more gradual approach to homozygosity permits a more effective elimination of them as they are discovered. Since lethal genes are apparently very widely distributed in chickens, utilization of very close inbreeding, while satisfactory for quickly increasing homozygosity, is often accompanied by unfavorable results which make the practice undesirable. Asmundson (1935) and Marsden and Knox (1937) have obtained similar results in inbreeding turkeys.

Line breeding involves the repetition of certain desirable individuals and their offspring in successive generations for the production of inbred strains. By this method a male may be mated to his daughters and then later to the female offspring resulting from the mating with his daughters. Similarly a female may be mated to her son and later to a male produced from the mating with her son. Line breeding attempts to concentrate the favorable qualities of an individual in a flock by inbreeding in the above manner.

Systems involving mating of less closely related individuals have been widely used and have produced good results. It is common practice to line-breed for several generations and also to mate individuals not more closely related than first cousins. Even in such matings, detrimental ef-

fects may be produced in some cases. But, if the stock is vigorous and has previously been selected for desirable characters associated with hatchability, growth, and viability, successful matings may be expected.

Outbreeding and Crossbreeding.—The opposite of inbreeding is involved in outbreeding and crossbreeding. In outbreeding, or outcrossing, birds of the same breed or variety but of nonrelated strains are mated. In crossbreeding, the birds are of different breeds or varieties. One type of outbreeding recently advocated (Waters, 1937) has involved topcrossing, in which two nonrelated strains are crossed and their offspring in turn mated to another strain not related to the first two. Frequently the strains so mated are themselves inbred to some degree, but after outbreeding to nonrelated strains, the degree of inbreeding as calculated on the basis of a reasonable number of generations is reduced to zero.

Outbreeding may be resorted to when some desirable characters are lacking in the strains bred. Its proper use involves the introduction of necessary genes into the strains to be improved. Care should be taken to make test matings to measure the results of the outcross before new stock is indiscriminately mated with known strains. The combination of characters from the crossing of genetically different strains at times gives rise to very favorable performance in the offspring (Warren, 1930), in which case the two strains are said to "nick," and at other times they may give an inferior type of offspring. Many strains of birds have been ruined by the unwise introduction of new stock by matings involving the whole flock, or the greater part of the best birds in the flock, without previous test of the progeny of such matings. On the introduction of new breeding strains into the flock, a number of test matings should be made and the progeny given a chance to prove their qualities before extensive matings between the two strains are attempted.

Successful crossbreeding requires the maintenance of two or more breeds or varieties with such characteristics that, when they are crossed, the first-generation offspring are superior to the parental stock (Warren, 1930). The product of the cross is said to show hybrid vigor and is of superior commercial value. These crossbred birds are not satisfactory breeders as a rule, and therefore the cross must be repeated when more crossbred stock is desired. The average poultry breeder has sufficient difficulties in breeding one strain of poultry without multiplying his work with more breeds or varieties. Only in cases where a large production of crossbred chicks is possible, does a sufficient emphasis on good breeding of the parental stock become warranted economically. Some breeds and strains are not suitable for crossing because they transmit undesirable characters to their offspring, and hybrid vigor does not result.

Grading.—When a flock is found to be deficient in many respects, a poultryman may resort to a system of grading. In this system, males are introduced each year from a superior strain or breed and are mated to successive generations of selected breeding hens until the flock comes to resemble more and more the quality of the superior birds purchased. Lippincott (1920) has shown that flocks of mongrel fowls can be rapidly improved by this system of breeding. It is also widely used by multipliers of commercial egg-production stock, who return each year to the same poultry breeder for breeding males.

A slight degree of inbreeding may be involved in the practice of grading, the extent depending on the relationship between the males purchased in different years. Such relationship is usually not sufficiently close to produce any detrimental effects and there is no reason to change to another strain of breeding males if satisfactory results have been obtained.

Value of Breeding Systems.—The purpose of inbreeding is to increase the uniformity of stock by increasing the number of pairs of genes in the homozygous condition. Outbreeding and crossbreeding, on the other hand, definitely increase heterozygosity and lead to less uniformity in breeding results in subsequent generations. If the poultry breeder desires to obtain a flock which will breed reasonably true for desired characters for a number of generations, then some degree of inbreeding must be involved. If the breeder desires only one generation of stock possessing a maximum of qualities for a specific purpose, then outbreeding or crossbreeding may produce the type of stock desired.

The success of various systems of poultry breeding rests not so much in the method chosen as in the use of records for the elimination of undesirable characters and selection of superior birds for mating. Blind adherence to any method is apt to lead to failure. The value of adequate records rests in the information made available to the breeder, who then can intelligently choose the system most likely to produce good results. The system, of course, may vary from year to year, with the quality of the stock available.

RELATION OF GENETICS TO POULTRY-BREEDING METHODS

Pedigree Breeding.—Knowledge of genetics can be applied to best advantage in the improvement of strains of poultry only with the aid of pedigree breeding. Information on the characters exhibited by individual birds must be supplemented by knowledge regarding the same characters in the ancestors of the mated birds in order to determine the

degree of probable homozygosity for desirable genes. The best test of a breeding bird's value is found in the performance of its progeny, the determination of which demands complete pedigree records. Other measures of the probable value of a breeding bird rely on the performance of the family of which the bird was a member. Here, too, pedigree records are required to establish relationship.

With adequate records of pedigree and of individual characteristics and with a knowledge of the principal genes concerned with egg production in birds, results to be expected in the offspring from a given mating may be predicted with a fair degree of accuracy. Once a mating is adequately tested and known to give good progeny, it may then be repeated as long as the original breeders give viable offspring with the knowledge that the future offspring will perform reasonably like their older brothers and sisters.

Pedigree breeding, coupled with a knowledge of genetics and progeny-test data, eliminates many of the hit-or-miss results obtained by other methods of mating in which the relationship of birds is not accurately known. It also makes possible more rapid improvement in specific hereditary characters which are controlled by several pairs of genes than can be obtained by simply selecting individuals showing the desired characters. Today, practically all of the leading breeders of egg-production strains of poultry pedigree their stock.

Pedigree Records.—Trapnesting, pedigreeing, and record keeping are futile if an analysis of records is not made in such a way as to reveal not only the best individual performances but also the best means of reproducing superior offspring. Record-keeping systems may be simple or complex according to the number of characters for which selection is practiced. Any system which demands so much work in its keeping that adequate analysis of records is prevented is a detriment to, rather than an aid in, breeding. The rule should be to simplify record taking to the point where further reduction in scope would eliminate essential information on characters of importance in the selections made.

We have often been asked to recommend record forms for pedigree breeders of poultry. In our opinion no one system of records is best for all breeding purposes. Pedigree breeders should be encouraged to develop their own record forms to meet their own needs. In any case, some form should be provided for each of the following: (1) daily egg-production record of individual birds, (2) hatching and chick-banding records, (3) mating records, and (4) family summaries. The latter should summarize the performance of individual members of each family with respect to the characters affecting production and viability. Wher-

ever possible, records of mortality and autopsy findings, as well as of quality characteristics of the birds and of the eggs produced, should be taken and summarized.

Sib and Progeny Testing.—Recent developments in breeding methods which have come into popular use involve the analysis of records of family performance. Males and females from families in which the sisters have made known records of performance are called "sister-tested." When records of growth, viability, feathering, and other characters are also available for the brothers of such individuals, the term "sib-tested" is used. The term "sib" here refers to the family of full brothers and sisters. Similarly the sires and dams which produced the family are called progeny-tested. The sib and progeny tests may reveal the family to be superior, average, or poor. These tests enable the selection of breeding stock from the superior individuals belonging to superior families. The genetic composition of breeding birds is more easily revealed by a study of family records than in cases where no sib or progeny data are available.

The value of sib, sister, and progeny tests depends partly on the number of offspring tested for each mating and partly on taking unselected groups of individuals for the tests. From matings which give a high degree of uniformity in production and viability of the offspring, as few as five pullet offspring may suffice for a reasonably accurate progeny test, especially when the hatching season is limited. More offspring are usually desired for matings giving a wider segregation of qualities; in these cases probably not less than ten should be tested. Any means of selection which tends to eliminate certain types of offspring from the test leads to a false measurement of the breeding value of the mated birds. Thus an accurate progeny, sister, or sib test demands an unselected and unculled group.

When data from accurate progeny tests are available, the breeder has eliminated a considerable factor of chance in results to be expected from repetition of matings. The egg production of the groups of offspring resulting from the same mating may vary in noninherited characters from year to year; also in cases where environmental conditions are known to interact with genes controlling inherited characters, variation between offspring produced in different years or seasons may occur. However, the greater part of the genetic control of production characters will be expressed alike in groups of pullets hatched in different years.

Table 6 gives some data on results obtained from the California Station flock on repeated matings. Despite considerable differences in environmental conditions during the years in which these data were taken, the

relative order of superiority of the matings was maintained. Unfortunately, data here presented are limited both in the number of repeated matings and in the number of daughters per mating. Frequently, production indexes of the daughters of a mated pair will vary in different years by 20 to 30 eggs or more. Rarely, however, will a mating that has proved to be superior in one year give inferior progeny in another year, or vice versa. Jull (1933*b*) has reported even closer agreement between groups of offspring produced by the same matings.

TABLE 6

PRODUCTION INDEXES OF PROGENY PRODUCED IN DIFFERENT YEARS FROM THE SAME MATINGS

Class by first year of mating	Number of matings	Year of mating	Number of daughters	Production index
100.1–125.0	2	First	16	108.6
		Repeated	15	114.7
125.1–150.0	2	First	21	149.6
		Repeated	17	170.9
150.1–175.0	0	——	—	——
175.1–200.0	5	First	62	187.4
		Repeated	37	174.9
200.1–225.0	3	First	24	207.9
		Repeated	20	185.6

The relative value of sister tests in breeding for egg production can be illustrated by data on the same flock involving a greater number of birds (table 7). While the individual egg-production record of the dam showed no correlation with the production index of the daughters, the production index of the family of full sisters including the dam bore a direct relation to the production index of the daughters. For this group of birds, the production of the dam's family of full sisters is certainly a better criterion of breeding value than the individual record of the dam. These results indicate the desirability of selecting good families from which good individuals may be chosen as breeders. However, Jull (1933*b*) has been able to find no correlation between the average production of full sisters of the dam and that of the daughters in his work. An explanation for the differences between Jull's results and ours in this respect is not available.

Whether or not the individual record of the dam bears any important relation to the production ability of the daughters has been strongly de-

bated. Jull (1933*b*) has found little or no correlation between dam's and daughters' egg-production records. In this respect, his results are similar to ours given in table 7. Goodale (1935), on the other hand, has found some correlation between the production of the dam and that of the daughters. These two conflicting reports and also the data given above can perhaps be reconciled to a certain degree. In Jull's data and in ours, the range of production of the dams was relatively narrow (between 200 and 300 eggs), while in Goodale's data a number of groups of dams had

TABLE 7

RELATION OF PRODUCTION INDEXES OF 262 WHITE LEGHORN PULLETS TO THE AVERAGE RECORD OF DAM AND TO THE AVERAGE PRODUCTION INDEX OF THE DAM AND HER FULL SISTERS

(Each group represents approximately one-quarter of the total number of pullets)

Classification by dam's record		Classification by family records	
Average record of dams	Production index of daughters	Average production index of dams and their full sisters	Production index of daughters
eggs			
287.6	183.4	230.3	215.1
270.5	214.4	201.0	213.0
250.2	191.0	191.6	205.0
226.6	185.3	108.5	139.2

produced less than 200 eggs and others had produced over 300 eggs. It still is possible to conclude that when the production of the dams is between 200 and 300 eggs, close correlation with daughters' records is often not obtained.

Another valuable use for progeny tests is found in connection with the introduction of new and unrelated breeding stock into a strain, as previously discussed under "Outbreeding and Crossbreeding" (p. 32).

Progeny testing is also of value in experimental matings. The number of such matings possible under commercial poultry-breeding conditions usually must be small. However, in the breeding of any flock, conditions will often arise which cannot be answered from previous experience. In these cases, the poultry breeder is justified in making matings designed to reveal new facts which will guide him in future breeding procedure.

Multiplication of Superior Stock.—The multiplier may buy superior stock from the pedigree breeder and reproduce it by generations of non-pedigree matings. His job is to increase the number of superior birds

available for commercial poultry keeping with as little loss of quality in the strain as possible. He may sell his products as pullets or adult stock to commercial poultrymen or as eggs to the hatcheries, which in turn sell baby chicks to the commercial poultrymen. In either case, the multiplier serves a very useful purpose: he brings the improvements gained by pedigree breeding within the means of the commercial poultryman, who often cannot afford to buy pedigreed stock for the production of market eggs, even if unlimited quantities were available. The multiplier who, by lack of an effective breeding program, makes no effort to improve the quality of his stock, is of doubtful service to the poultry industry.

TABLE 8

Production and Mortality with Respect to Quality of White Leghorn Pullets as Determined at Five Months of Age

Grade at 5 months of age	Total number of birds	Per cent of flock	Production index	Per cent pathology
1	263	24.4	182.2	40.3
2	783	72.7	150.9	48.5
3	31	2.9	62.8	77.4
All grades	1,077	100.0	156.0	47.3

The males used in multipliers' flocks should be from pedigreed ancestry. The most rapid dissemination of good qualities can only be obtained by mating superior males with selected hens. The females can be culled frequently or trapnested for short periods of time in order to select the superior individuals. In flocks where the pullets will later be used for breeders, a constant selection of stock should be practiced from hatching time until the matings are made. Birds showing retarded development should be eliminated throughout the growing period. At 5 to 6 months of age, the pullets should be graded and segregated according to their development. First-grade birds will, on the average, prove to be the best stock. Second-grade birds often are profitable commercially but do not average as well as the first-grade stock. Third-grade birds are underdeveloped and should be culled, because they rarely prove profitable even under favorable commercial conditions.

Table 8 gives production and mortality data on three grades of birds from the California Station flock. This type of results has been repeatedly obtained in grading birds over a period of years. Profitable levels of production were reached only in the first and second grade. Pathological conditions in the first and second grades were lower than in the third grade.

Segregation into grades as here used was based on the comparative development of the birds. In the first grade, only birds of good size and weight, without coarseness, with good pigmentation of shanks and beaks (in case of yellow-skinned breeds), and showing freedom from any apparent disease, were included. The second grade consisted of birds not so well developed as those in the first grade but also apparently free from disease. The third grade included all small birds, as well as those with poor pigmentation and those showing signs of the onset of pathological conditions. One of the most frequent of these was the beginning of blindness produced by an iritis.

While many birds belonging to the second grade will make good production records, the character of their development should cause hesitation about their promiscuous use as breeders. A strain of birds characterized by rapid and sturdy growth is desired in commercial poultry production. Under the same flock conditions, the first-grade pullets develop in a superior manner and, provided they meet all other standards, are to be preferred as breeders. Third-grade birds should be marketed as poultry meat or destroyed.

Where circumstances prevent the trapping of potential breeding birds for a complete year of production, trapping for a period of two to three months is a valuable aid in selection of stock. When combined with the use of culling methods, part-time trapnesting can be used to determine with good accuracy the productive ability of a bird. It is particularly valuable for determining the ability of the bird to lay at a rapid rate, which cannot be established by culling methods alone. However, culling methods can be used to determine with reasonable accuracy the length of time a bird lays if applied during usual periods in which the birds are maturing, pausing, or molting.

A Breeding Program for Multipliers.—While it is not considered advisable to present a rigid program of breeding procedure for pedigree breeders, because of the variability of conditions encountered in different flocks, a general breeding program for multipliers may be advanced. Such a program can be presented in the form of a summary of the preceding discussion. The application of the following specific recommendations should be limited to birds hatched in the spring season, from February to April:

1. Remove all poorly developed birds at any stage of development.

2. Segregate the pullets at five to six months of age and discard all birds falling into the third grade.

3. If part-time trapnesting can be used for birds aged six to eight months, eliminate pullets laying at less than 65 per cent net rate. This

procedure will also enable elimination of individuals producing undesirable types of eggs.

4. Remove late-maturing or pullet-molting birds from the breeding flock in November or December of the first laying year.

5. Remove all birds which become broody in the course of the year.

6. Cull the flock in the summer or early fall to eliminate early molters and poor producers, as determined by the usual methods of judging past production.

7. Remove all diseased birds and pullorum reactors.

8. Mate selected females to sib- or sister-tested pedigreed males from high-production stock which also exhibits high viability under commercial flock conditions.

9. Do not set small, overly large, misshapen, poor-shelled, or off-colored eggs.

Age of Breeding Stock.—The comparative value of young and old birds as breeders is frequently debated. If natural selection operates to remove the weaker birds and if these birds were weak owing to genetic causes, then older birds should unquestionably be superior to the young birds of the same flock as breeders. However, the individuality of birds frequently does not reveal their complete genetic constitution. Even in families with low average viability, there are often individuals which live to an advanced age. In numerous instances in the California Station flock, these birds have given offspring with poor viability. Age, in itself, is no guarantee of the ability of an individual to transmit high viability to its offspring. On the other hand, a flock of old birds should have been reduced by culling and natural selection to the point where its offspring should excel offspring from the same flock before the poorer and weaker individuals had been eliminated. So far as is known, the same bird possesses the same ability to transmit desirable inherited characters to its offspring when it is a pullet as at any later time in its life (Hays, 1928), although a change in the incidence of certain diseases may greatly affect the amount of mortality in the offspring from different years of mating.

In commercial stock produced without the aid of pedigree records, breeding from older hens and cocks is advisable unless younger stock from strains characterized by superior viability are available. Where pedigrees are known, family characteristics and proved breeding ability rather than age of the breeding bird should be the decisive factors.

WHAT BREEDING CAN ACCOMPLISH

As previously stated, many characters of production and viability in poultry appear to result from the interaction of genetic and environmental factors. Improvement in any flock may represent actual increase in number of desirable genes or it may be merely the reflection of improved nutrition, disease-control methods, or management. Munro (1937) has given strong evidence that much of the improvement in average egg production attributed to breeding selection is not genetic in origin. Certainly no one can dispute the fact that improvements in knowledge of poultry nutrition during the last two decades have made possible a better average winter egg production than was previously attainable.

To present concrete evidence for an undiluted effect of breeding selection, all controllable nongenetic influences must be kept constant as far as is possible; or, if they do vary, their effect must be measured independently from the effect of the genes. Such conditions have prevailed for a number of years in the Single Comb White Leghorn breeding flock of the University, and it is possible to state that no environmental changes associated with nutrition or management can account for the results obtained, with the exception of an improvement in early growth and sexual maturity obtained by nutritional means. The results presented in table 9 thus give a reasonably accurate measure of the effect of the breeding selections practiced for all except the above-mentioned characters.

Egg Production.—As can be seen, a rather unusual improvement in the average productive level of the flock was obtained. Associated with the improvement in number of eggs produced were earlier sexual maturity, higher rate, higher persistency as measured by age at last egg, and a reduced pathology. No material improvement with respect to broodiness was obtained except in the last two years of mating. While the amount of winter pausing was reduced, improvement was not consistently obtained. The amount of spring and summer pausing, however, was greatly reduced. The improved production was not associated with any sacrifice of desirable egg size or egg color.

During the years represented by the data in table 9, improvement was obtained in family lines originally represented in the first year of the study, as well as in new families originating from purchased stock crossed with the foundation lines. Whether the stock originated from families present in the original flock or from crosses with other strains, the progeny produced was submitted to an analysis of production characters and family performance before any further use as breeders was made of the parents. Of five males from other strains which were mated

with selected hens of the Station flock in the course of these years, two were proved satisfactory by the progeny test for continuation in the breeding flock. In the case of the three unsatisfactory males, only a few progeny were saved for breeding. Since matings headed by males not

TABLE 9

PRODUCTION AND PATHOLOGY CHARACTERISTICS OF THE CALIFORNIA STATION FLOCK OF PRODUCTION-BRED SINGLE COMB WHITE LEGHORNS

	1933	1934	1935	1936
Number of pullets banded	535	704	485	403
Average weight at banding time	2.59 lbs.	2.65 lbs.	2.98 lbs.	2.90 lbs.
Average date of first egg	Nov. 12	Oct. 13	Oct. 4	Sept. 16
Average age at first egg	211 days	195 days	187 days	174 days
Per cent of birds maturing under 200 days of age	43 p.ct.	64 p.ct.	71 p.ct.	84 p.ct.
Per cent of birds with high rate*	46 p.ct.	52 p.ct.	76 p.ct.	73 p.ct.
Per cent of birds with winter pause, 7 days or longer	67 p.ct.	65 p.ct.	45 p.ct.	52 p.ct.
Per cent of birds with spring or summer pause, 7 days or longer	54 p.ct.	37 p.ct.	37 p.ct.	34 p.ct.
Per cent of birds broody	15 p.ct.	18 p.ct.	13 p.ct.	9 p.ct.
Average date of last egg†	Oct. 13	Oct. 4	Oct. 8	Oct. 17
Average age at last egg†	546 days	551 days	557 days	566 days
Per cent of birds laying October 1 at end of pullet year	50 p.ct.	67 p.ct.	54 p.ct.	69 p.ct.
Per cent of birds attaining 2-oz. egg size	72 p.ct.	74 p.ct.	76 p.ct.	79 p.ct.
Per cent of birds laying creamy eggs	2 p.ct.	3 p.ct.	3 p.ct.	2 p.ct.
Per cent pathology to September 1‡ (17 months of age)	38.3 p.ct.	32.7 p.ct.	27.8 p.ct.	33.8 p.ct.
Per cent pathology to October 1‡ (18 months of age)	55.0 p.ct.	38.1 p.ct.	36.8 p.ct.	36.5 p.ct.
Per cent reproductive pathology for year§	22.0 p.ct.	14.3 p.ct.	14.2 p.ct.	18.6 p.ct.
Per cent neoplastic pathology for year§	10.6 p.ct.	9.1 p.ct.	8.9 p.ct.	6.7 p.ct.
Per cent digestive pathology for year§	19.2 p.ct.	7.1 p.ct.	6.8 p.ct.	4.7 p.ct.
Per cent functional pathology for year§¶	16.2 p.ct.	10.6 p.ct.	10.3 p.ct.	10.7 p.ct.
Average 365-day egg record of survivors	217 eggs	234 eggs	239 eggs	243 eggs
Hen-day average for 365 days	175.6 eggs	206.6 eggs	241.9 eggs	249.7 eggs
365-day production index	126.3	170.0	186.0	196.0
Production index to October 1 (average age of pullets, 18 months)	125.6	171.8	186.5	201.6

* See figure 4 for definition of high rate.

† Records closed on January 15.

‡ Records based on original number of pullets banded at five months of age. The difference between pathology to September 1 and that to October 1 largely represents the proportion of the flock culled in September which showed pathological lesions.

§ Includes mortality and birds disposed of at the end of the year which showed pathological lesions. The figures for different types of pathology are nonadditive, since many duplications exist.

¶ Largely degeneration of the kidney and liver.

bred by us accounted for less than 20 per cent of the total matings in the years cited, the whole improvement in the flock cannot be attributed to outbreeding with birds of other strains. However, a valuable hereditary contribution was made by the two introduced males which proved to be satisfactory.

Viability.—During this period the flock has been free from all known infectious diseases except coccidiosis which, however, caused the death of a very few birds and was a minor pathological factor. The preceding statement does not refer to neuro- and visceral lymphomatosis, the infectiousness of which has not been demonstrated for this flock (Beach, 1938). Yet the proportion of the flock showing pathological conditions has not been low.

An examination of the types of pathology present in this flock emphasizes the importance of loss from diseases or functional disturbances of unknown origin and for which no means of control has been devised

TABLE 10

OCCURRENCE OF NEOPLASTIC DISEASES IN THE OFFSPRING PRODUCED FROM MATINGS OF BIRDS FROM FAMILIES SHOWING FREQUENT OCCURRENCE OF NEOPLASMS

Year	Number of birds	Per cent neoplasms
1933-34	52	13.5
1934-35	129	25.5
1935-36	152	27.6
1936-37	134	23.9

(Lubbehusen and Beach, 1938). Reproductive and functional types of mortality have not been specifically selected against. Losses from pathology associated with the digestive system in the 1933 flock were unusually high and were found predominantly in the families from one male and his son. After elimination of these families, losses from disorders of the alimentary system dropped sharply for the succeeding years.

Neoplastic diseases (including neurolymphomatosis, lymphoid infiltration of organs, iritis, tumors, etc.) have declined slowly during the four years reported. At the same time, deliberate efforts were made to breed a strain of birds susceptible to these neoplasms. Data in table 10 indicate that deliberate breeding of birds from families showing a frequent occurrence of neoplasms may result in increasing losses from pathology of this kind. Birds produced from these matings received the same rations and management as those from the production-bred line in which a decrease in incidence of neoplasms has occurred (table 9). In fact, birds from high- and low-mortality selections were hatched in the same incubators, reared in the same brooders, and kept in the same laying houses for their first year of production. Yet while, in the production-bred flock, a decrease occurred in the proportion of birds exhibiting neo-

plasms, the families shown in table 10, after a marked first-year increase, maintained approximately the same higher level of neoplastic pathology. The evidence from these matings indicates a possible genetic basis for susceptibility or resistance to certain neoplastic diseases. Similar evidence has been obtained by Williams, Gildow, and Lampman (1938) and Wilcke, Lee, and Murray (1938). Probably either the hereditary basis for resistance is complex or it involves complicated interactions with nongenetic influences.

Breeding for disease resistance is slow and costly. Where adequate means are available to control diseases by means of agglutination tests, vaccines, specific drugs, or sanitation, trying to breed for resistance is uneconomic. Where no means of control are available and where there are evidences of different responses by birds of different strains or families, genetic selection is advisable, even though improvement of the stock comes slowly.

Some poultrymen are prone to suggest that, if birds are properly selected and mated, strains will be created with such inherent vigor that they can withstand adverse conditions commonly found on poultry ranches. But this seems more than can logically be expected to result from good breeding. Inadequate or deficient rations, insanitary conditions, and generally poor management cannot be overcome by better breeding of poultry.

Importance of Other Conditions.—In presenting the results obtained with the California Station flock, we have attempted to show how identification of and selection for characters of production and viability have resulted in improved average egg production in successive generations. Poultry breeding is but one means for improvement of conditions in poultry production. As such, its contribution must be added to the contributions from other sciences as applied to poultry for the solution of the problems which the poultryman faces in his business. Breeding can create stock with improved potentialities for profitable production, but such potentialities will not be realized unless the birds are well fed, housed, and managed. Good breeding probably will not help the inefficient poultryman; it can expand the possibilities for success on the part of the poultryman whose methods of feeding and flock management are sound.

LITERATURE CITED

Asmundson, V. S.

1927*a*. A study of first year egg production of S. C. Rhode Island Reds. Sci. Agr. 8:141–50.

1927*b*. A study of the changes in the distribution of first year eggs within a flock of S. C. White Leghorns at the University of British Columbia. Proc. 3d World's Poul. Cong. [Ottawa]. p. 129–37.

1928. The first year egg production of Barred Plymouth Rocks. Sci. Agr. 9:90–102.

1935. Some results of turkey breeding work at the California Agricultural Station. California Turkey News. August; p. 3–4.

1938. Influence of various factors on egg production in turkeys. Jour. Agr. Res. 56:387–93.

Asmundson, V. S., and J. Biely.

1930. Effect of pullorum disease on distribution of first year egg production. Sci. Agr. 10:497–507.

1932. Inheritance of resistance to fowl paralysis (neurolymphomatosis gallinarum) I. Differences in susceptibility. Canad. Jour. Res. 6:171–76.

Axelsson, J.

1936. Untersuchungen über die Form der Hühnereier. Proc. 6th World's Poul. Cong. [Leipzig]. 2:1–4.

Beach, J. R.

1938. Experiments in the transmission of fowl lymphomatosis by inoculation. Poultry Sci. 17:67–71.

Benjamin, E. W.

1920. A study of selections for the size, shape and color of hens' eggs. N. Y. Agr. Exp. Sta. (Cornell) Mem. 31:195–312.

Bissonnette, T. H., and A. G. Csech.

1937. Hatching pheasant chicks on Christmas day. Amer. Nat. 71:525–28.

Buckner, G. D., J. H. Martin, and W. M. Insko, Jr.

1930. Some chemical factors governing egg formation in the hen. Proc. 4th World's Poul. Cong. [London]. Sec. B; p. 330–33.

Byerly, T. C., and W. H. Burrows.

1936. Studies of prolactin in the fowl pituitary. II. Effects of genetic constitution with respect to broodiness on prolactin content. Proc. Soc. Exp. Biol. and Med. 34:844–46.

Clark, L. B., S. L. Leonard, and G. Bump.

1937. Light and the sexual cycle of game birds. Science 85:339–40.

Cole, L. J., and J. G. Halpin.

1922. Results of eight years of inbreeding Rhode Island Reds. Anat. Rec. 23:97.

Dryden, J.

1921. Egg-laying characteristics of the hen. Oregon Agr. Exp. Sta. Bul. 180:1–96.

Dunkerly, J. S.

1930. The effect of inbreeding. Proc. 4th World's Poul. Cong. [London]. Sec. A; p. 48–71.

Dunn, L. C.

1922. The relationship between weight and the hatching quality of eggs. Connecticut (Storrs) Agr. Exp. Sta. Bul. 109:92–114.

1923. Experiments on close inbreeding in fowls. Connecticut (Storrs) Agr. Exp. Sta. Bul. 111:139–72.

GILDOW, E. M., J. K. WILLIAMS, and C. E. LAMPMAN.
1936. The transmission of fowl paralysis (lymphomatosis) Poultry Sci. **15**:244–48.

GOODALE, H. D.
1918. Internal factors influencing egg production in the Rhode Island Red breed of domestic fowl. Amer. Nat. **52**:65–94, 209–32, 301–21.
1935. Relationships between egg production of ancestors and offspring. Poultry Sci. **14**:295.

GOODALE, H. D., R. SANBORN, and D. WHITE.
1920. Broodiness in domestic fowl. Data concerning its inheritance in the Rhode Island Red breed. Massachusetts Agr. Exp. Sta. Bul. **199**:93–116.

GREENWOOD, A. W.
1932. The value of progeny in relation to age of dam. Harper-Adams Utility Poultry Jour. **17**:478–80.

HALL, G. O.
1935. The value of the pedigree in breeding for egg production. Poultry Sci. **14**: 323–29.

HALL, G. O., and A. VAN WAGENEN.
1936. The association of certain measures of interior egg quality with hatchability. Poultry Sci. **15**:501–6.

HAYS, F. A.
1924. Inbreeding the Rhode Island Red fowl with special reference to winter egg production. Amer. Nat. **58**:43–59.
1928. Relation of age of parents to hatchability, livability and fecundity in the domestic fowl. Poultry Sci. **7**:106–15.
1929. The inheritance of egg weight in the domestic fowl. Jour. Agr. Res. **38**: 511–19.
1936*a*. Inheritance of sexual maturity in Rhode Island Reds. Proc. 6th World's Poul. Cong. [Leipzig]. **2**:34–38.
1936*b*. Studies on the inheritance of persistency. Genetics **21**:519–24.
1937. Inheritance of egg size and egg character. Massachusetts Agr. Exp Sta. Bul. **344**:1–28.

HAYS, F. A., and R. SANBORN.
1924. The inheritance of fertility and hatchability in poultry. Massachusetts Agr. Exp. Sta. Tech. Bul. **6**:20–42.
1926. Annual persistency in relation to winter and annual egg production. Massachusetts Agr. Exp. Sta. Tech. Bul. **9**:190–203.
1932. Types of intensity in Rhode Island Reds. Massachusetts Agr. Exp. Sta. Bul. **286**:1–11.
1934. Breeding for egg production. Massachusetts Agr. Exp. Sta. Bul. **307**:1–27.

HOLST, W. F., and H. J. ALMQUIST.
1931. Measurement of deterioration in the stored hen's egg. Hilgardia **6**(3):49–60.

JULL, M. A.
1932. Poultry breeding. 376 p. John Wiley and Sons, Inc., New York, N. Y.
1933*a*. Inbreeding and intercrossing in poultry. Jour. Heredity **24**:93–101.
1933*b*. Progeny testing in poultry breeding as a means of evaluating the breeding potentiality of an individual. Amer. Nat. **67**:500–14.

KEMPSTER, H. L., and J. E. PARKER.
1936. The normal growth of chickens under normal conditions. Missouri Agr. Exp. Sta. Res. Bul. **247**:1–47.

Knox, C. W.

1930. Factors influencing egg production. I. The influence of maturity upon egg production in S. C. White Leghorns. Iowa Agr. Exp. Sta. Res. Bul. **119**: 311–32.

Knox, C. W., and A. B. Godfrey.

1934. Variability of thick albumen in fresh-laid eggs. Poultry Sci. **13**:18–22.

Knox, C. W., M. A. Jull, and J. P. Quinn.

1935. Correlation studies of egg production and possible genetic interpretations. Jour. Agr. Res. **50**:573–89.

Kopeć, S.

1924. Some data referring to size, shape and weight of eggs in the domestic fowl. Pam. Państ. Inst. Nauk. Gosp. Wiejsk. Puławach. (Mém. Inst. Natl. Polon. Écon. Rurale Puławy) **5**:294–327.

Lambert, W. V., and C. W. Knox.

1932. Selection for resistance to fowl typhoid in the chicken with reference to its inheritance. Iowa Agr. Exp. Sta. Res. Bul. **153**:262–95.

Landauer, W.

1937. The hatchability of chicken eggs as influenced by environment and heredity. Connecticut (Storrs) Agr. Exp. Sta. Bul. **216**:1–84.

Lerner, I. M., and L. W. Taylor.

1936. The relation of pauses to rate of egg production. Jour. Agr. Res. **52**:39–47.

1937*a*. The measurement of sexual maturity and persistency. Poultry Sci. **16**: 419–21.

1937*b*. The spurious nature of the linkage between length of laying year and sexual maturity in the fowl. Amer. Nat. **71**:617–22.

Lippincott, W. A.

1920. Improving mongrel farm flocks through selected standard-bred cockerels. Kansas Agr. Exp. Sta. Bul. **223**:1–48.

Lorenz, F. W., and H. J. Almquist.

1935. Firm white of fresh and storage eggs. Poultry Sci. **14**:340–41.

1936. Seasonal variations in egg quality. Poultry Sci. **15**:14–18.

Lorenz, F. W., L. W. Taylor, and H. J. Almquist.

1934. Firmness of albumen as an inherited characteristic. Poultry Sci. **13**:14–17.

Lubbehusen, R. E., and J. R. Beach.

1938. Poultry mortality of non-infectious origin. Jour. Amer. Vet. Med. Assoc. (In press.)

Marsden, S. J., and C. W. Knox.

1937. The breeding of turkeys. Yearbook of Agriculture **1937**:1350–66.

Munro, S. S.

1937. Inheritance of egg production in the domestic fowl. II. Increases in production, their extent and characteristics with a discussion of causal factors. Sci. Agr. **17**:376–85.

1938. Effect of heredity on interior egg quality and shell composition. Poultry Sci. **17**:17–27.

Pearl, R.

1912. The mode of inheritance of fecundity in the domestic fowl. Jour. Exp. Zool. **13**:153–268.

1923. Duration of life as an index of constitutional fitness. Poultry Sci. **3**:1–10.

PEARL, R., and F. M. SURFACE.
1909. Data on the inheritance of fecundity obtained from the records of egg production of the daughters of "200-egg" hens. Maine Agr. Exp. Sta. Bul. 166:49–84.

PETROV, S. G.
1935. Analysis of the development of high and low lines of Leghorns at Cornell. Poultry Sci. 14:330–39.

PUNNETT, R. C.
1923. Heredity in poultry. 204 p. Macmillan and Co., London.
1933. Genetic studies in poultry. IX. The blue egg. Jour. Genet. 27:465–70.

RICE, J. E.
1914. Some practical points in the management of poultry for egg production. Massachusetts State Board of Agr. Bul. 1:106–37.

RIDDLE, O., R. W. BATES, and E. L. LAHR.
1935. Prolactin induces broodiness in fowl. Amer. Jour. Physiol. 111:352–60.

ROBERTS, E., and L. E. CARD.
1926. The inheritance of resistance to bacillary white diarrhea. Poultry Sci. 6: 18–23.
1934. The inheritance of broodiness in the domestic fowl. Proc. 5th World's Poul. Cong. [Rome]. 2:353–58.
1936. Inheritance of resistance to bacterial infection in animals. Illinois Agr. Exp. Sta. Bul. 419:467–93.

SCOTT, H. M., and L. F. PAYNE.
1937. Light in relation to the experimental modification of the breeding season of turkeys. Poultry Sci. 16:90–96.

TAYLOR, L. W., and J. H. MARTIN.
1928. Factors influencing thickness of egg shell. Poultry Sci. 8:39–44.

UPP, C. W., and B. A. TOWER.
1936. The incidence of blindness and paralysis according to family. Poultry Sci. 14:421.

VAN WAGENEN, A., and G. O. HALL.
1936. The inheritance of certain characters affecting egg quality. Poultry Sci. 15:405–10.

WARREN, D. C.
1930. Crossbred poultry. Kansas Agr. Exp. Sta. Bul. 252:1–54.
1934. Inheritance of age at sexual maturity in the domestic fowl. Genetics 19: 600–617.

WATERS, N. F.
1937. The use of inbred fowls for top-crossing. Poultry Sci. 16:348.

WATERS, N. F., and W. V. LAMBERT.
1936. Inbreeding in the White Leghorn fowl. Iowa Agr. Exp. Sta. Res. Bul. 202: 1–55.

WILCKE, H. L., C. D. LEE, and C. MURRAY.
1938. Susceptibility and resistance of some strains of chickens to fowl leucosis. Poultry Sci. 17:58–66.

WILLIAMS, J. K., E. M. GILDOW, and C. E. LAMPMAN.
1938. Some factors influencing the transmission of fowl paralysis. U. S. Egg and Poultry Mag. 44:24–27.

18m-10,'38(4013)